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PHOTOSYNTHATE ALLOCATION AND SOIL NITROGEN; A MODEL STUDY

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Abstract

The hypothesis of optimal allocation of photosynthates was tested at different levels of soil nitrogen. A model for the growth and nitrogen uptake of the plant was constructed with the aid of the following assumptions: 1) The photosynthetic rate of a plant depends on nitrogen concentration and dry-weight of above-ground parts. 2) The nitrogen uptake rate of a plant is proportional to soil nitrogen concentration and to the amount of roots. 3) The photosynthetic products are immediately consumed in growth. 4) Soil nitrogen concentration as well as the allocation ratio of photosynthates are both constant. According to the model, the final size of a plant strongly depends on the allocation ratio of photosynthates. The allocation ratio of photosynthates giving the maximal size was determined. The predictions of the model correspond qualitatively to the experimental results.

INTRODUCTION

The effect of fertilizers on the growth and functioning of plants is well documented in the literature. The results presented are mostly experimental observations. One can ask, however, why the measured relationship is like this. That is, what could be the mechanisms causing the observed relationship. It is clear, that if information concerning mechanisms can be obtained, it is of great value in unifying the bulk of experimental data into a framework. The mechanisms can be described with the aid of models and, with them, the consequences of different alternatives can be tested.

In this case, a study (Sievänen et al. 1983) on the determination of the allocation ratio of photosynthates in a plant (Salix cv. "Aquatica") is presented. The study is based on a simple model describing growth and nitrogen uptake of a plant. A hypothesis is made that the plant functions according to a rule "to maximize its own size" and with the aid of the model the consequence of this hypothesis is derived for the allocation of photosynthates at varying soil nitrogen contents.

The model

The plant is considered as consisting of two parts, the above-ground and the below ground (roots). The following are the main assumptions of the model:

1. The photosynthetic rate of a plant depends on nitrogen concentration and dry-weight of above-ground parts.
2. The nitrogen uptake rate of a plant is proportional to soil nitrogen content and to the amount of roots.
3. The photosynthetic products are immediately consumed in growth.
4. Soil nitrogen concentration as well as the allocation ratio of photosynthates are both constant during the growing period.

With the aid of the assumptions the equations for growth and nitrogen uptake of the plant can be derived. First, let α denote the fraction of photosynthates that are allocated to roots, M the amount of nitrogen taken up, N_s the nitrogen content of the soil, n the nitrogen content of the above-ground parts and W_s and W_r the dry-weights of the above-ground and below ground parts, respectively. Then, the growth rates of plant parts and the amount of nitrogen taken up are given by;

$$\frac{d}{dt} W_s = (1-\alpha) f(n) W_s$$

$$\frac{d}{dt} W_r = \alpha f(n) W_s$$

$$\frac{d}{dt} M = \beta N_s W_r$$

where β is a constant and f is a function which describes the dependency of the photosynthetic rate on the nitrogen content of the above-ground parts. The shape of function f has been derived from related experiments.

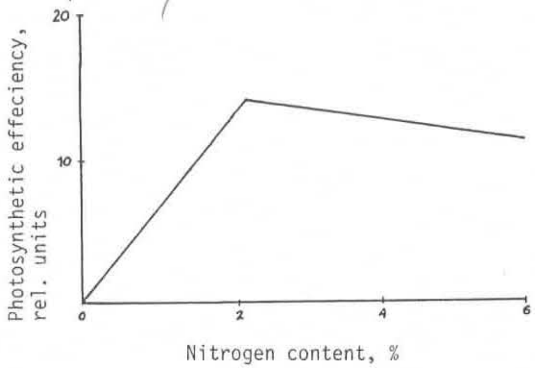


Fig. 1. Function used in the model for the dependency of the photosynthetic rate on the nitrogen content of the above-ground parts.

The nitrogen taken up is consumed differently in the above-ground and below ground parts. It can be assumed that the share of nitrogen taken up which is used in each plant part depends on average chemical composition and relative growth rate of the parts. With the aid of these assumptions and the above equations the fraction of uptaken nitrogen flowing to above-ground parts, m_s, can be given by

$$m_s = \frac{a(1-\alpha)}{a+b\alpha},$$

where a and b are parameters which depend on the chemical composition of the plant. For the total amount of nitrogen in above-ground parts, M_s, it holds that

$$\frac{d}{dt} M_s = m_s \beta N_s W_r.$$

Now, with the aid of the M_s value the nitrogen content of above-ground parts is obtained;

$$n = \frac{M_s}{W_s}.$$

The equations given above describe the growth and nitrogen uptake of a plant during one growing period.

Optimal photosynthate allocation

According to the model the dry-weight of a plant depends strongly on the allocation ratio of photosynthates, Fig. 2. The value of the allocation ratio giving maximum size for the plant is clearly dependent on soil nitrogen content (Fig. 2).

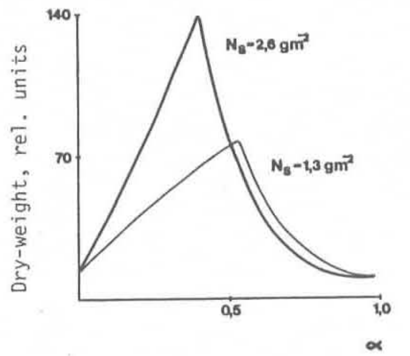
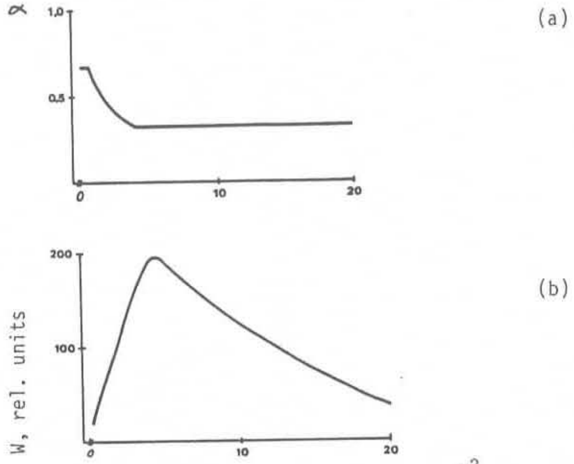


Fig. 2. Dry-weight of the plant, computed with the aid of the model, at the end of one growing period as a function of the allocation ratio of photosynthates at two soil nitrogen contents.

It can be often argued that in certain circumstances it is preferable for a plant to attain a large size. Such a situation arises, for example, when plants are competing for limited space. When the size of the plant at the end of the growing period is used as a criteria of optimality and the value of the optimal allocation ratio of photosynthates is calculated for varying soil nitrogen contents, the result is Fig. 3a. In the derivation of the optimum value it has been assumed that there exists a certain limit, below which the allocation ratio cannot fall without injuring a plant's other functions (water uptake etc.). When the allocation ratio given in Fig. 3a is applied, the resultant total dry-weight of the plant behaves according to Fig. 3b.



Nitrogen concentration in the soil, N_s, g m^{-2}

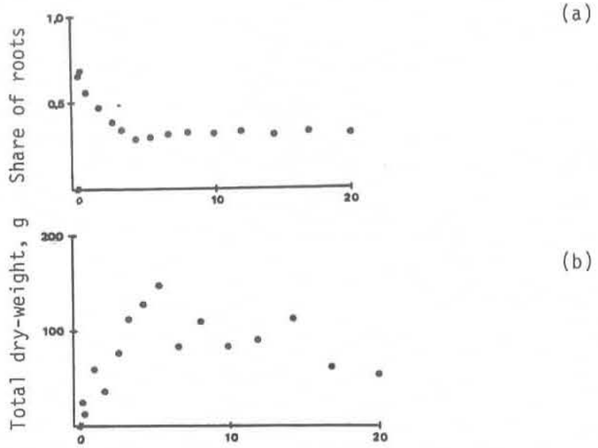
Fig. 3 (a) The optimal allocation ratio of photosynthates as a function of the soil nitrogen content.

(b) Dry-weight of a plant at the end of the growing period when the optimal allocation ratio of photosynthates is applied.

The curves in Fig. 3 depend on the value of the parameters applied. When relevant values for parameters are used, however, the general shapes of the curves remain unchanged. That is, the optimal allocation ratio of photosynthates is strongly increasing with the decreasing soil nitrogen content (at small values) and the curve for the dry-weight of the plant shows a peak. These qualitative features are thus characteristic of the optimal solution for the allocation ratio of photosynthates in the circumstances described, under assumptions 1-4.

A related experiment

Willow cuttings were subjected for one growing period to a varying nitrogen supply. Each cutting was kept, as accurately as possible, at a constant soil nitrogen content. The plants were analysed at the end of the growing period with results according to Fig. 4.



Initial nitrogen concentration in the soil N_s, g m^{-2}

Fig. 4 (a) The ratio of dry-weight of the roots and the total plant dry-weight at end of the growing period as a function of the initial nitrogen content of the soil (according to the experiment).

(b) Dry-weight of a plant in the experiment as a function of the initial nitrogen content of the soil.

CONCLUSIONS

It is seen that the curves predicted with the aid of the model have similar shapes to the experimental results (see Figs 3, 4). Above it has shown that if assumptions 1-4 cover the essential features of the growth condition of a plant, the allocation ratio of photosynthates (given in Fig. 3a) results in the maximal size of the plant. The reseblance of the theory to experiment thus suggests that in certain circumstances the functioning of a plant can be understood by "the optimality hypothesis". It has to be kept in mind, however, that there can be several rules for functioning which lead to the same actual result in certain circumstances (e.g. the shoot-root equilibria (Richards et al. 1979)).

This study also clarifies the mechanism causing an increase in growth when nutrients are added to the soil (at low nutrient levels); when the nutrient content of the soil is increased, the nutrient content of the plant (especially the above-ground parts) is increased and the allocation of photosynthates to above-ground parts in increased too (Fig. 4a). Both these phenomena enhance the photosynthesis and thus growth. Therefore, with plants, the effect of adding nutrients is two-fold, the photosynthetic efficiency is increased and the structure is changed so that faster growth is possible.

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